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Modulation of the eyeblink and cardiac startle reflexes by genuine eye contact

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Abstract

Is another person's direct gaze an inherently positive or negative stimulus? The present study employed the startle reflex methodology to investigate individuals' automatic reactions to another person's direct and averted gaze. In the study, participants' eyeblink startle and cardiac reflexes elicited by a high-intensity acoustic noise stimulus were measured in the context of viewing a live model's direct and downward gaze. Both the eyeblink electromyographic and electrocardiographic data revealed that the startle reflex was modulated by gaze direction. Direct gaze attenuated the eyeblink startle and cardiac reflexes to the acoustic probes compared to those elicited in the context of a downward gaze. These results indicate that the defense reflex is weaker when presented in the context of direct versus downward gaze, and thus suggest that another individual's direct gaze, compared to averted gaze, automatically elicits more positive affective responses in the viewer.

KEYWORDS

affective evaluation, direct gaze, heart rate, implicit response, startle reflex

1 INTRODUCTION

Prior research investigating affective evaluations of eye gaze in various social contexts has suggested that direct gaze can be either a positive social signal or a negative stimulus signaling threat or dominance (Argyle & Cook, 1976; Kleinke, 1986). Previous laboratory-based experiments have attempted to minimize and control the effects of contextual social factors, but they have also reported somewhat inconsistent findings regarding the affective evaluation elicited by direct gaze. For example, studies measuring self-reported affective responses to eye gaze have reported less positive evaluations to direct gaze versus averted gaze and closed eyes, both when showing pictures of animated faces as well as faces of real people as stimuli (Chen, Helminen, & Hietanen, 2016; Chen, Peltola, Ranta, & Hietanen, 2016; Hietanen, Leppänen, Peltola, Linna-aho, & Ruuhiala, 2008; Pönkänen, Alhoniemi, Leppänen, & Hietanen, 2011). On the other hand, other studies have shown that faces with direct gaze are evaluated as more likable, and elicit more positive feelings than faces with averted gaze (Kuzmanovic et al., 2009; Mason, Tatkow, & Macrae, 2005; Wirth, Sacco, Hugenberg, & Williams, 2010). It is possible that the discrepant results reflect differences in the stimulus materials (e.g., live faces vs. facial images; static gaze vs. dynamic gaze shifts) or measurements (e.g., evaluations of subjective affective valence vs. liking ratings of the stimulus faces). For example, likability ratings are likely to be influenced by perceived politeness and trustworthiness of a face. Thus, it is possible that a face with direct gaze is perceived as more polite and trustworthy as compared to a face with averted gaze, and, therefore, it would be rated as more likable. Instead, the ratings of subjective feelings of pleasantness may be influenced, for example, by the effects of gaze direction on self-awareness. Seeing another's direct gaze has been shown to increase self-directed attention (Hietanen & Hietanen, 2017), and self-focused attention may lead, via critical evaluation of the self, to an aversive state (Duval & Wicklund, 1972). Additionally, in the studies reporting

less positive evaluations to direct than averted gaze (Chen, Helminen, & Hietanen, 2016; Chen, Peltola et al., 2016; Hietanen et al., 2008; Pönkänen, Alhoniemi et al., 2011), static images were employed, whereas the other previous studies employed dynamic gaze stimuli with a gaze shift or an eyeblink (Kuzmanovic et al., 2009; Mason et al., 2005; Wirth et al., 2010). It is possible that a static direct gaze may be interpreted as dominant and staring and, therefore, less positive than averted gaze. All these factors may have contributed to differences in explicit rating results notoriously known to be susceptible to task demands, motivational biases, and other top-down influences (Evans, 2008; Hofmann, Gawronski, Gschwendner, Le, & Schmitt, 2005; Nosek, Hawkins, & Frazier, 2011).

One possibility to tackle this problem is to investigate implicit responses instead of explicit evaluations. Implicit responses may better reflect perceivers' instinctual reactions to direct gaze. Recently, we employed the affective priming paradigm to investigate individuals' implicit affective reactions to eye gaze (Chen, Helminen, & Hietanen, 2016; Chen, Peltola et al., 2016). In these studies, direct gaze, averted gaze, and closed eyes stimuli were briefly presented as primes immediately followed by positive and negative words as targets. The participants were required to evaluate the valence of the words as quickly as possible. The results showed that positive words were categorized faster when preceded by direct gaze than when preceded by closed eyes primes, whereas negative words were categorized faster when preceded by closed eyes versus direct gaze primes. The affective priming effect has been interpreted to indicate that the presentation of the prime automatically activates the associated affective evaluation and facilitates the processing of affectively congruent targets (Fazio, 2001; Klauer & Musch, 2003). Thus, the results were interpreted to indicate that the perception of direct gaze automatically activates more positive evaluations than closed eyes (Chen, Helminen, & Hietanen, 2016; Chen, Peltola et al., 2016). Another prior study using the Implicit Association Test provided compatible findings by showing a robust preference for faces looking toward the perceiver rather than faces looking away (Lawson, 2015).

Psychophysiological measures indexing physiological reactions associated with psychological states provide an alternative approach to investigate individuals' implicit affective responses to gaze stimuli. For instance, previous studies have repeatedly reported that direct gaze, as compared with averted gaze or closed eyes, elicits larger skin conductance response (SCR) and greater relative left-sided frontal EEG activity (Helminen, Kaasinen, & Hietanen, 2011; Hietanen et al., 2008; Kylliäinen et al., 2012; Nichols & Champness, 1971; Pönkänen, Peltola, & Hietanen, 2011). These measures indicate that, relative to averted gaze and closed eyes, direct gaze enhances affective arousal and elicits a motivational approach tendency in viewers (Harmon-Jones, 2003; Helminen et al., 2011; Hietanen et al., 2008; Kylliäinen et al., 2012; Pönkänen, Peltola, & Hietanen, 2011). However, these measures are not able to unequivocally index the valence of the affective reactions. SCRs reflect affective arousal but not affective valence, and although motivational approach tendencies are related to positive affective experiences, approach-related negative emotions, such as anger, can also elicit relatively greater left-sided frontal EEG activity typically associated with approach motivation (Harmon-Jones, 2003).

In order to further examine implicit affective reactions to direct gaze, in the present study, we employed the startle reflex methodology. The startle reflex is an automatic defensive reaction to sudden and intense stimuli, and it is typically investigated by measuring electromyographic (EMG) eyeblink responses triggered by an acoustic startle probe (Bradley, Cuthbert, & Lang, 1999; Grillon & Baas, 2003; Lang, Bradley, & Cuthbert, 1990). Importantly, prior studies have repeatedly shown that the magnitude of the startle reflex is modulated by the affective valence of simultaneously presented emotional stimuli. Eyeblink startle reflex is augmented in an aversive context (e.g., while watching disgust-inducing pictures) and attenuated when elicited in a pleasant context (e.g., Bradley & Lang, 2000; Bradley, Lang, & Cuthbert, 1993; Roy, Mailhot, Gosselin, Paquette, & Peretz, 2009; Vrana, Spence, & Lang, 1988). The modulation of the startle reflex by an affective context has been replicated in many studies using various types of affective foreground stimuli, including

pictures (Bradley, Lang, & Cuthbert, 1993; Vrana et al., 1988), films (Jansen & Frijda, 1994), sounds (Bradley & Lang, 2000; Roy et al., 2009), and odors (Miltner, Matjak, Braun, Diekmann, & Brody, 1994). The startle reflex modulation can be observed even during imagery of affective sentences (Cook, Hawk, Davis, & Stevenson, 1991; Vrana & Lang, 1990). The robustness of this effect has made it a valuable tool in probing the valence dimension of foreground stimuli (Bradley et al., 1999; Grillon & Baas, 2003; Lang et al., 1990). In fact, there is previous evidence from one study that gaze direction can modulate the magnitude of the startle reflex. In this study, male participants were shown photographs of nude females with direct and averted gaze as foreground stimuli (Lass-Hennemann, Schulz, Nees, Blumenthal, & Schachinger, 2009). The results showed that, as expected, the nude bodies attenuated the magnitude of the startle reflex, but the attenuation was smaller in the context of direct than averted gaze. The authors suggested that the direct gaze attracted attention away from the nude bodies to the faces, thus reducing the influence of the nude bodies on startle reflex. However, because, in that study the gaze direction stimuli were embedded in affective pictures with high positive affective valence, it is still an open question whether another person's gaze direction as such modulates the magnitude of the startle reflex.

In addition, we also measured heart rate (HR) responses to the startle probes. Previous studies have reported initial increases in HR (within 10 s) following startle stimulus (Graham, 1992; Holand, Girard, Laude, Meyer-Bisch, & Elghozi, 1999; Richter et al., 2011). The cardiac acceleration response has also been suggested to index a defensive reflex (Graham & Clifton, 1966). Presentation of a sudden and intense stimulus activates both somatic and autonomic defense reflexes (Sánchez et al., 2009). The neural circuits of different defense reactions share common modulatory structures, with the central nucleus of the amygdala as the key pathway to those subcortical and brain stem areas that control the defense reactions (Vila et al., 2007). This suggests that both eyeblink and cardiac startle reflexes would be modulated by affective foreground stimuli. Indeed, previous studies have reported the modulation of the

cardiac startle response by affective context. Cardiac acceleration responses elicited by intense noise stimuli are potentiated by the presentation of unpleasant and phobia-related pictures and attenuated by pleasant pictures (Ramírez et al., 2010; Richter et al., 2011; Ruiz-Padial, Mata, Rodríguez, Fernández, & Vila, 2005; Sánchez et al., 2009).

In the present study, we measured participants' eyeblink startle and cardiac reflexes elicited by an abrupt and loud white noise in the context of viewing a live model's direct and downward gaze. Based on our previous affective priming studies showing direct gaze automatically eliciting more positive responses, we expected that eyeblink startle reflexes to the noise bursts would be attenuated during viewing direct gaze as compared to viewing downward-looking gaze. Due to the robust nature of the affective startle modulation, the present study provides a critical test for the hypothesis proposing that direct gaze is a positive affective signal. Moreover, as suggested by the studies of Vila and colleagues (for a review, see Vila et al., 2007), we expected that the presentation of the startle probe would elicit a cardiac acceleration response peaking around the third second after the probe onset. Importantly, according to previous studies investigating the affective modulation of cardiac startle reflex, we expected that the cardiac acceleration response elicited by the startle probes would be smaller in the context of direct versus downward gaze. After the startle task, we also asked the participants to rate the affective valence and arousal of their subjective feelings to each gaze stimulus in order to examine their explicit responses to gaze direction.

2 METHOD

2.1 Participants

The sample consisted of 32 participants (25 female, age range 17–33 years, mean age = 21 years), who were high school and university students recruited via mailing lists. The inclusion criteria were normal or corrected-to-normal vision and, according to participants' self-report, absence of psychiatric diagnoses. All participants gave a written, informed consent, and received course credits or a movie ticket for their participation. Due to technical errors, three participants were excluded from the eyeblink EMG and one participant from the HR data analyses. One participant was excluded from the valence rating data analyses and two participants from the arousal rating analyses due to incomplete data. Ethical statement for the study was obtained from the Ethics Committee of the Tampere region, and the study conformed to the Code of Ethics of the World Medical Association (Declaration of Helsinki).

2.2 Stimuli and procedure

The stimulus persons were two female and two male models. Each participant was presented with one model of the same sex. During the trials, the models had a neutral expression and kept their faces as motionless as possible throughout the experiment. The instruction was to maintain a slight muscle tonus in the lower part of the face in order not to look sullen or fatigued and to avoid eyeblinks. However, when necessary, eyeblinks were allowed to occur. The models' gaze was directed either directly at the participant or downward, while head orientation remained frontal in both conditions. The face stimuli were presented through a 30 × 40 cm custom-built electronic shutter with a voltage sensitive liquid crystal (LC) window (NSG UMU Products Co., Ltd.) attached to a black frame between the model and the participant (Figure 1, left). The participant was seated at a distance of 80 cm from the LC shutter, and the model was sitting at a distance of 40 cm from the shutter. The model's seat was adjusted in such a way that his/her eyes were at the same level vertically with the participant's own eyes. The state of the LC

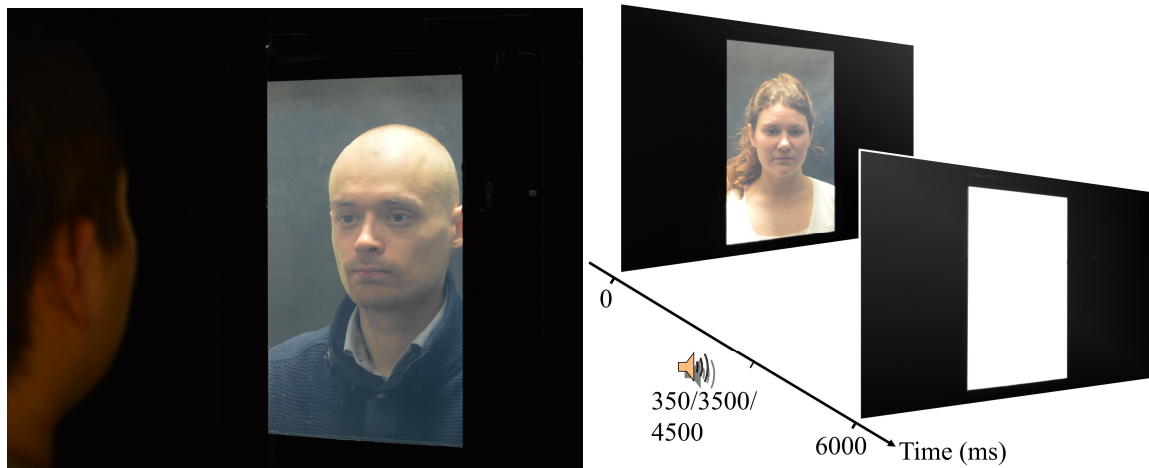


FIGURE 1 Left: Experimental setup. Participant with the recording electrodes attached viewing a stimulus person behind the LC shutter. Right: Events of a single trial. Shutter window was transparent for 6,000 ms, during which the stimulus person's face with either direct or downward gaze was presented. An acoustic probe was presented 350 ms, 3,500 ms, or 4,500 ms after the gaze stimulus onset.

shutter (transparent or opaque) was operated by E-Prime 2.0 software (Psychology Software Tools, Pittsburgh, PA) running on a desktop computer, and the LC shutter switched between opaque and transparent states within an overall speed of 3 ms.

Upon arrival to the laboratory, the recording electrodes were attached, and the participant was given 4 min to acclimate in the recording environment. The experimenter explained that the purpose of the study was to measure physiological responses to a simple interaction with another person. The person displaying the face stimuli (i.e., model) then entered the room and was introduced to the participant. Next, the experimenter described that the window in front of the participant will occasionally open and the participant will see the model for a few seconds. The participant was instructed to look directly at the model and avoid unnecessary movements. In addition, occasional sounds would be presented through the headphones, and the participant was instructed to ignore these sounds. The participant then put on the headphones, and the experiment began.

The duration of each trial was 6,000 ms during which the shutter window was transparent and the model's direct or downward gaze remained constant (Figure 1, right). A

computer-controlled intertrial interval (from offset to onset) was randomized between 15 s and 20 s. During the trials, startle responses were triggered by presenting a 95-dB white noise sound for 500 ms binaurally through headphones. To increase the unpredictability of the startle stimulus, the sound was presented with three stimulus onset asynchrony (SOA) conditions of 350 ms, 3,500 ms, or 4,500 ms after the gaze stimulus onset. The experiment included 64 trials in one block with half of the trials presenting direct gaze and the other half presenting downward gaze. The order of gaze presentation was randomized. For each gaze condition, the startle probe was presented randomly with each SOA for eight times and was absent in the rest of the trials. An additional 16 startle stimuli were presented randomly during the interstimulus intervals to further increase temporal unpredictability and break a specific association between face presentations and startle stimuli. Therefore, responses to the nontrial startle stimuli were not included in the analysis.

After presentation of the experimental trials, the headphones were removed and participants filled in a brief questionnaire to evaluate their explicit affective responses to the two gaze conditions. The shutter window was switched to be transparent for 6,000 ms twice to show the participants the direct and downward gaze, with the order of the gaze stimuli counterbalanced across participants. After both stimulus displays, the participants evaluated their own sentiments of affective valence and arousal to each gaze stimulus on a 9-point Self-Assessment Manikin (SAM, see Bradley & Lang, 1994) scale (1 = *unpleasant/calm*, 9 = *pleasant/arousing*).

2.3 Physiological data recording and reduction

Eyeblink startle responses were measured by recording EMG activity with bipolar 4-mm Ag/AgCl electrodes attached 1 cm apart over the left orbicularis oculi muscle and a ground electrode attached to the forehead (Fridlund & Cacioppo, 1986). The signal was amplified by a QuickAmp amplifier and recorded with BrainVision Recorder software (Brain Products GmbH, Munich, Germany) with a 500-Hz sampling rate. Offline, the EMG signal was band-

pass filtered at 28–500 Hz and rectified using BrainVision Analyzer 2.1 software. The data were then segmented to epochs to include EMG signal 50 ms before and 300 ms after each startle stimulus presented during both gaze conditions. The segments were visually inspected for artifacts, and epochs containing excessive muscle activity or blinks during the 50-ms baseline period (5% of all epochs) were excluded from further analyses. Startle responses were then quantified by detecting the peak amplitude within 20–300 ms poststimulus from which baseline EMG activity (i.e., average amplitude of the 50-ms baseline period) was subtracted. These scores were then averaged for each SOA and gaze condition.

Electrocardiogram (ECG) was recorded with bipolar electrodes attached to the left and right arm using the same apparatus as with the EMG recording. Offline, an in-house, MATLAB-based software was used to identify R peaks in the ECG signal. In order to investigate cardiac reactions to the startle stimulus during viewing different gaze directions, the HR data were segmented into 6,500-ms epochs starting 500 ms prior to the startle stimulus onset. Within data segments, manual correction was used, when necessary, to correct for falsely detected or missing R peaks. Segments with excessive distortion in the ECG signal (1%) were excluded. For the accepted segments, interbeat intervals (IBIs; i.e., the time intervals between two successive R peaks) were quantified and assigned to 500-ms intervals by weighting each IBI by the proportion of the 500-ms interval occupied by that IBI. Finally, IBIs were converted to beats per minute (BPM) and averaged across different trials within each gaze and SOA condition. The analyses were performed with HR change scores, which were calculated by subtracting the baseline BPM during the 500 ms preceding the startle stimulus onset from each of the BPMs during the 500-ms intervals after the startle onset. Thus, positive HR change scores indicated HR acceleration, and negative scores indicated HR deceleration.

2.4 Statistical analysis

As the time interval between the two long SOAs (3,500 ms and 4,500 ms) was short and there was no reason to expect the physiological responses to differ across these two conditions, the two longer SOAs were combined in the analysis of the EMG and HR data. The eyeblink EMG data (raw values) were first normalized with log10 transformation and then entered in a repeated analysis of variance (ANOVA) with gaze direction (direct and downward gaze) and SOA (short and long SOAs) as within-subject factors. A 2 (Gaze Direction) \times 2 (SOA) \times 12 (Time Interval) repeated ANOVA was performed on the HR data. For the SAM rating data, two-tailed paired t tests were conducted to test differences in the valence and arousal ratings between the direct and downward gaze conditions. Huynh-Feldt correction for violations of sphericity was applied where appropriate. For the sake of clarity, uncorrected degrees of freedom are reported. All statistical analyses were performed using the SPSS package.

3 RESULTS

3.1 Startle reflex

The analysis of the startle blink magnitudes revealed significant main effects of gaze direction and SOA. Overall, smaller blink magnitudes were elicited by the startle probe when viewing direct gaze ($M = 77.9 \mu V$, $SEM = 12.2$) as compared with downward gaze ($M = 87.7 \mu V$, $SEM = 11.4$), $F(1, 28) = 6.37$, $p = .018$, $\eta_p^2 = .185$. Regarding SOA, blink magnitudes were larger at the long SOA ($M = 88.8 \mu V$, $SEM = 11.9$) than at the short SOA ($M = 76.9 \mu V$, $SEM = 11.5$), $F(1, 28) = 7.95$, $p = .009$, $\eta_p^2 = .221$. The interaction between gaze direction and SOA was also significant, $F(1, 28) = 4.49$, $p = .043$, $\eta_p^2 = .138$. Further paired t tests showed that the blink response magnitudes did not differ for direct versus downward gaze at the short SOA, $t(28) = -0.63$, $p = .534$, Cohen's $d = 0.05$, whereas the blink response magnitudes were significantly larger for downward than direct gaze at the long SOA, $t(28) = -3.67$, $p = .001$, d

= 0.54. Figure 2 depicts the pattern of blink modulation as a function of gaze direction and SOA.

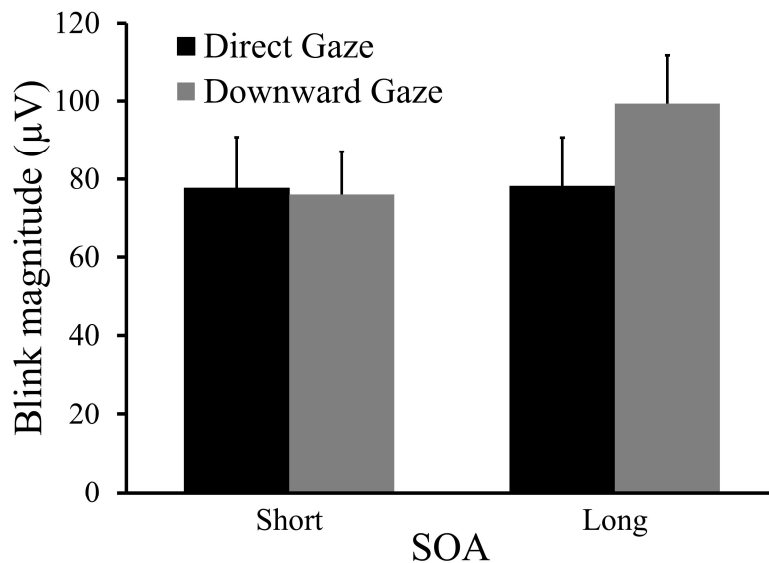


FIGURE 2 Mean blink magnitudes to the startle probe when viewing direct and downward gaze at the short and long SOAs. Error bars represent one standard error above the mean

3.2 Heart rate response

The ANOVA on heart rate responses revealed a significant main effect of gaze direction, $F(1, 30) = 5.87, p = .022, \eta_p^2 = .164$. Specifically, the HR response was significantly greater when viewing downward gaze ($M = 1.10, SEM = 0.25$) than when viewing direct gaze ($M = 0.51, SEM = 0.28$). Additionally, the results showed a main effect of SOA condition, $F(1, 30) = 28.00, p < .001, \eta_p^2 = .483$. The HR response was greater for the long SOA ($M = 1.82, SEM = 0.27$) than for the short SOA ($M = -1.22, SEM = 0.48$). The interaction between gaze direction and SOA was not significant ($p = .987$). The interaction between SOA and time interval was also significant, $F(11, 330) = 26.78, p < .001, \eta_p^2 = .472$, reflecting a tendency for HR deceleration as a function of time at the short SOA (a classic HR orienting response, Graham & Clifton, 1966), but HR acceleration (defense response) at the long SOA. There was no significant main effect of time interval ($p = .317$) or interaction between gaze direction and

time interval ($p = .093$). Figure 3 depicts the pattern of HR changes as a function of gaze direction across the SOA conditions.

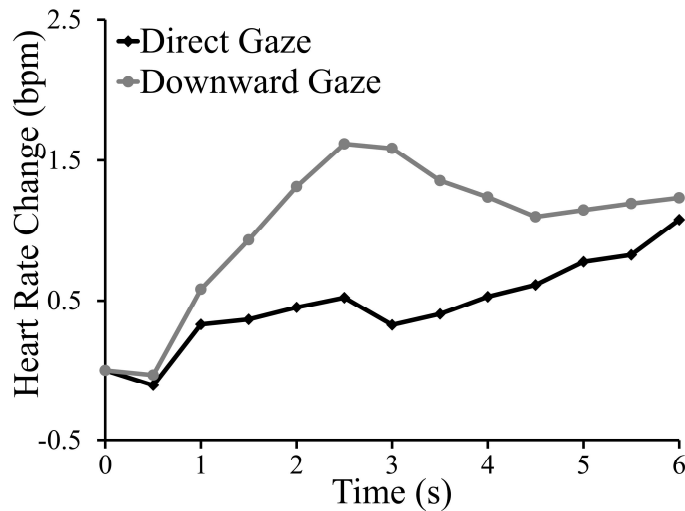


FIGURE 3 Mean HR changes to the startle probe when viewing direct and downward gaze within the 6-s time interval across the short and long SOAs

3.3 SAM ratings

For the valence ratings, a paired t test showed that direct gaze ($M = 5.52$) was rated as slightly less positive than downward gaze ($M = 5.81$), but this difference was not significant, $t(30) = -0.75$, $p = .461$, $d = 0.13$. For the arousal ratings, the analysis showed that direct gaze ($M = 4.63$) was rated as significantly more arousing than downward gaze ($M = 3.57$), $t(29) = 2.49$, $p = .019$, $d = 0.45$.

4 DISCUSSION

By employing the startle reflex methodology, the main aim of the present study was to investigate automatic affective reactions to another person's gaze direction. The psychophysiological data revealed that another person's gaze direction indeed modulated the viewers' eyeblink and cardiac startle reflexes. Presentation of a sudden and intense acoustic stimulus activated smaller eyeblink startle and smaller cardiac acceleration responses in the context of direct versus downward gaze. To our knowledge, the present study is the first to examine the eyeblink and cardiac startle reflexes while viewing a live person's gaze, and it

adds to the startle reflex literature by showing modulation of these reflexes by seeing another person's face with varying gaze direction. The eyeblink reflex and the acceleration of heart rate immediately after the onset of the startle stimulus have been suggested to be associated with defense reflexes to protect individuals from the effects of aversive stimuli (Graham, 1992; Graham & Clifton, 1966; Lang et al., 1990). Furthermore, previous studies investigating the eyeblink startle reflex with various types of affective foreground stimuli have demonstrated a robust affect-startle effect: Startle reflex is potentiated in an unpleasant context and reduced when elicited in a pleasant context (for reviews, Bradley et al., 1999; Grillon & Baas, 2003; Lang et al., 1990). Likewise, the cardiac startle reflex is also modulated by the affective context, with greater cardiac acceleration responses during unpleasant and phobia-related contexts compared to those evoked during pleasant contexts (Ramírez et al., 2010; Richter et al., 2011; Ruiz-Padial et al., 2005; Sánchez et al., 2009).

Ruiz-Padial et al. (2005) suggested that the affective modulation of both eyeblink and cardiac startle responses can be interpreted by Lang's motivational priming model (see also Ramírez et al., 2010; Sánchez et al., 2009). Specifically, the motivational priming hypothesis suggests that emotional behaviors are driven by two motivational systems, one appetitive and one defensive. In this view, the defensive startle reflex is automatically primed by unpleasant stimuli, such as affectively negative pictures, which signal a threat to the organism's survival and thus activate the defensive motivational system. By contrast, this reflex is inhibited by pleasant stimuli, such as erotic pictures, which promote survival and thus activate the appetitive system (Bradley, Codispoti, Cuthbert, & Lang, 2001; Lang, 1995; Lang et al., 1990; Lang, Bradley, & Cuthbert, 1998). Therefore, the present psychophysiological results are interpreted to indicate that direct gaze, relative to downward gaze, is automatically perceived as a more positive social signal, thus attenuating the startle reflex to intense sound stimuli. These results and conclusions are in line with those from our previous studies using the affective priming paradigm (Chen, Helminen, & Hietanen, 2016; Chen, Peltola et al., 2016).

Instead of affective modulation of the startle reflex, one might speculate whether the modulation could reflect attentional influences. An attentional account would suggest attenuation of the startle reflex by the amount of attentional resources allocated to the context stimuli. Thus, greater attenuation of the startle reflex in the context of direct than averted gaze could result from greater allocation of attention to direct gaze and, thus, decreased attention to the acoustic probe eliciting the startle reflex. However, this explanation is not likely. First, previous studies have suggested that attention may play a role in attenuating the startle reflex to probes presented shortly after the onset of the context stimulus, but not to probes presented with a longer delay after the context stimulus. It is a common finding that the magnitude of the eyeblink reflex is reduced if the probe is shortly preceded (30–500 ms) by another stimulus (prepulse inhibition, PPI; for a review, see Li, Du, Li, Wu, & Wu, 2009). The PPI is suggested to reflect a protective function of “gating out” the following extraneous stimulus (probe) and maintaining the processing of the first (context) stimulus (Braff, Geyer, & Swerdlow, 2001; Li et al., 2009). However, Bradley, Cuthbert, and Lang (1993) have investigated the startle reflex with acoustic probes presented at various delays after the foreground picture onset and suggested that the influences of attention and affect on the startle reflex follow different time courses (see also Robinson & Vrana, 2000). Specifically, they have suggested that attention explains the startle reflex attenuation to probes presented with short delays after foreground stimuli (SOAs shorter than 300 ms); but at longer delays (SOAs longer than 800 ms), when the foreground stimuli have been recognized and encoded, the defensive or appetitive motivational system is activated and modulates the reflex. Second, a previous study from our laboratory showed that discrimination of peripheral, irrelevant visual stimuli presented after live faces (using the same methodology as in the present study) was more enhanced after direct than averted gaze (Hietanen, Myllyneva, Helminen, & Lyyra, 2016). The result was explained by the effect of direct gaze on arousal and attention. Thus, if the startle reflex modulation in the present study had

reflected the attention effects, we should have observed greater eyeblink responses after direct than averted gaze. But as shown, the result was exactly the opposite.

Another potential explanation for the observed results is that the modulation of the startle reflex reflects the effects of the foreground stimulus on the participant's arousal. Studies investigating modulatory effects of affective arousal on the startle reflex have reported a potentiated startle reflex in the context of foregrounds with high arousal, such as imagery of very joyful or fearful scenes (Dillon & LaBar, 2005; Witvliet & Vrana, 1995, 2000). For the present study, however, this explanation does not hold either. As discussed above, another individual's direct gaze has been shown to be more arousing than averted gaze, indexed by both physiological and self-reported measures (Helminen et al., 2011; Hietanen et al., 2008; Myllyneva & Hietanen, 2015; Pönkänen, Alhoniemi et al., 2011). In the present study, the arousal ratings were also higher for direct than downward gaze. Thus, if the arousal hypothesis were correct, a potentiated startle reflex after direct gaze should have been observed. As noted above, this was not the case. To sum, we conclude that the valence account, rather than the attention or arousal account, is more tenable in explaining the startle modulation observed in the present study.

Finally, the behavioral results revealed that direct gaze was rated as slightly but not significantly less positive but significantly more arousing than downward gaze. These findings are in accord with previous studies showing that live faces with direct gaze were evaluated as less positive and more arousing than those with averted gaze and closed eyes (Hietanen et al., 2008; Pönkänen, Alhoniemi et al., 2011). Thus, compatible with previous studies (Chen, Helminen, & Hietanen, 2016; Chen, Peltola et al., 2016), the present results also showed that implicit (physiological) and explicit (self-evaluative) affective responses to another's gaze direction may not always be fully concordant.

An obvious limitation of the present study is the lack of a neutral context condition. Therefore, we cannot unconditionally determine whether the eyeblink and cardiac startle response modifications were due to a decreased response magnitude when viewing direct gaze,

an increased reflex when viewing downward gaze, or both. The present results revealed only the relative difference in the startle reflex magnitudes modulated by direct and downward gaze. Thus, the present findings could be accounted for by suggesting that downward gaze was perceived as a negative social signal, for example, a signal of social exclusion, and thus potentiating the startle response magnitudes. However, there are features in the pattern of the present results which, together with evidence from earlier research, suggest that direct gaze might have attenuated the eyeblink response. From the pattern of the startle reflex results depicted in Figure 2, it can be seen that the blink magnitudes in response to acoustic probes presented after downward gaze were greater at the long SOA than those at the short SOA, whereas the blink magnitudes after direct gaze were not different between the long and short SOAs. At first sight, one might interpret these findings to provide evidence in support of an increased startle reflex magnitude after downward gaze. However, as described above, besides the emotional modulation of the blink response at the long SOA, the eyeblink reflex is reduced by attentional effects at the short SOA (Li et al., 2009). The magnitude of the startle reflex has been shown to be greater at the long versus short SOAs in the context of viewing pleasant, neutral, and unpleasant pictures (Bradley, Cuthbert, & Lang, 1993; Graham, Putnam, & Leavitt, 1975; Li et al., 2009). Thus, based on these findings one could expect that, without an emotional modulation, the blink magnitudes after direct gaze should have been greater at the long versus short SOA. Instead, the present results showed no differences in the magnitude of the blink response after the direct gaze foreground stimulus when the probe was presented at the short versus long SOA. Therefore, one could argue that direct gaze elicited a positive affective reaction and attenuated the blink response from what it would have been without the effect of a positive affect.

We want to emphasize, however, that it is impossible to give a definitive answer to this question without a neutral condition. Unfortunately, selection of an appropriate neutral foreground stimulus is a notoriously difficult task (see Jonides & Mack, 1984). It is by no

means obvious what kind of a gaze stimulus would be “neutral.” Preselection of a neutral foreground gaze stimulus is, moreover, complicated by the fact that, as seen in previous research and the present study, explicit affective evaluations and implicit affective reactions do not necessarily result in compatible findings. One possibility to conquer this limitation in future research could be to use an incremental priming method that uses a within-condition baseline with gradually increasing prime intensity (e.g., luminance) or duration (Jacobs, Grainger, & Ferrand, 1995; Ziegler, Ferrand, Jacobs, Rey, & Grainger, 2000). With this method, without a neutral stimulus, the magnitude of the startle reflex could be measured in the context of direct and averted gaze stimuli as a function of the foreground stimulus luminance or duration. If direct gaze is an affectively positive stimulus, the magnitude of the startle reflex should decrease as a function of the luminance or duration of direct gaze foregrounds, and compatibly, if averted gaze is an affectively negative stimulus, the magnitude of the startle reflex should increase as a function of the luminance or duration of averted gaze foregrounds.

4.1 Conclusion

By measuring participants’ eyeblink and cardiac reflexes to loud acoustic noise stimuli, the present study revealed that the viewers’ startle reflexes were modulated by the contextual presentation of another person’s gaze direction. Presentation of the startle stimulus activated smaller eyeblink and cardiac acceleration responses in the context of direct versus downward gaze. These results are interpreted to indicate that defensive startle reflexes triggered by unpredictable aversive stimuli are weakened during moments of eye contact and suggest that direct gaze may be an inherently positive social signal.

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